

The University of Chicago

**THE ENDOCRANIAL BLOOD VESSELS
OF AMBLYSTOMA TIGRINUM**

AN EXPANSION OF A DISSERTATION SUBMITTED
TO THE FACULTY OF THE DIVISION OF THE
BIOLOGICAL SCIENCES IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ANATOMY

1934

By
PAUL GIBBONS ROOFE

Private Edition, Distributed by
THE UNIVERSITY OF CHICAGO LIBRARIES
CHICAGO, ILLINOIS

Reprinted from
THE JOURNAL OF COMPARATIVE NEUROLOGY
Vol. 61, No. 2, 1935

The University of Chicago

THE ENDOCRANIAL BLOOD VESSELS OF AMBLYSTOMA TIGRINUM

AN EXPANSION OF A DISSERTATION SUBMITTED
TO THE FACULTY OF THE DIVISION OF THE
BIOLOGICAL SCIENCES IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ANATOMY

1934

By
PAUL GIBBONS ROOFE

Private Edition, Distributed by
THE UNIVERSITY OF CHICAGO LIBRARIES
CHICAGO, ILLINOIS

Reprinted from
THE JOURNAL OF COMPARATIVE NEUROLOGY
Vol. 61, No. 2, 1935



THE ENDOCRANIAL BLOOD VESSELS OF AMBLYSTOMA TIGRINUM

PAUL GIBBONS ROOFE

*Hull Laboratory of Anatomy, The University of Chicago*¹

TWELVE FIGURES

(Accepted for publication June 14, 1934)

CONTENTS	
Introduction	258
Endocranial arteries	260
Arteria basilar	263
Arteria carotis	267
Ramus hy	267
Ramus me	267
Ramus co	269
Ramus co	270
Arteria caroti	270
Ramus h	270
Ramus h	271
Ramus h	271
Arteriae	273
Quantitative	274
Endocranial vein	276
Paraphysis,	276
Saccus endo	277
Dural veins	279
Veins of the brain	281
Vena hemisphaerii dorsalis	281
Vena hemisphaerii ventromedialis	281
Venae chorioideae	283
Venae taeniae	283
Vena hemisphaerii posterior	285
Vena prosencephali lateralis	285
Vena mesencephali	285

¹ This research was aided by the William Wilder, Jr. Fellowship in Neurology in The University of Chicago, and by a grant to The University of Chicago by the Rockefeller Foundation.



THE ENDOCRANIAL BLOOD VESSELS OF AMBLYSTOMA TIGRINUM

PAUL GIBBONS ROOFE

*Hull Laboratory of Anatomy, The University of Chicago*¹

TWELVE FIGURES

(Accepted for publication June 14, 1934)

CONTENTS

Introduction	258
Endocranial arteries	260
Arteria basilaris	263
Arteria carotis cerebialis, ramus posterior	267
Ramus hypothalamicus	267
Ramus mesencephali superior	267
Ramus communicans posterior	269
Ramus communicans cum a. basilari	270
Arteria carotis cerebialis, ramus anterior	270
Ramus hemisphaerii ventralis	270
Ramus hemisphaerii medialis	271
Ramus hemisphaerii posterior	271
Arteriae chorioideae	273
Quantitative pattern of arterial blood supply	274
Endocranial vein	276
Paraphysis, dorsal sac, and nodus vasculosus	276
Saccus endolymphaticus	277
Dural veins	279
Veins of the brain	281
Vena hemisphaerii dorsalis	281
Vena hemisphaerii ventromedialis	281
Venae chorioideae	283
Venae taeniae	283
Vena hemisphaerii posterior	285
Vena prosencephali lateralis	285
Vena mesencephali	285

¹ This research was aided by the William Wilder, Jr. Fellowship in Neurology in The University of Chicago, and by a grant to The University of Chicago by the Rockefeller Foundation.

Vena hypothalamica	285
Vena basilaris anterior	286
Vena basilaris posterior	286
Vena terminalis	286
Sinus obliquus	286
Sinus jugularis	288
Discussion and summary.....	288

INTRODUCTION

This paper presents the results of study by gross dissection and microscopic preparation of sixty adult specimens of *Amblystoma tigrinum*. The blood vessels have been investigated by several methods: first, by serial microscopic sections through the entire head; second, by microscopic sections variously prepared of the brain with pial vessels intact; third, by gross dissection; and fourth, by direct observation of the circulation in the living animal with the aid of a quartz rod transillumination from 500 and 1000 watt lamps, the concentration of the light to the rod being brought about by an ordinary substage microscope condenser.

In some cases the blood vessels were injected; in other specimens vessels naturally filled with blood gave satisfactory views of many details. After many experiments the most complete injections were obtained with carmine gelatin (Bensley's). This was injected by gravity at an average pressure of 75 cm. of water. The specimens that gave the best results were killed in fumes of amyl nitrite and allowed to remain 12 hours before injection, thus insuring complete relaxation of the arterial musculature. Injection was through the conus arteriosus, after clamping off the pulmonary arteries, the dorsal aorta dorsally of the apex of the ventricle, and the axillary arteries. By dissection under the microscope, injected vessels, both arteries and veins were followed easily and accurately.

The most complete account of amphibian endocranial vessels is that of the frog by Ecker, Wiedersheim, Gaupp (1899), and their nomenclature is the basis of that here employed; yet the vessels of *Urodela* differ so widely from those of *Anura* that comparisons are difficult. The published ac-

counts of endocranial blood vessels of urodeles are few and incomplete. The differences between the species described are great, variability of the vessels in specimens of the same species is surprisingly wide, and the names given to these vessels by different authors have little in common. Accordingly, the descriptive terms here adopted carry no implications of homologies with blood vessels of other vertebrate classes. The nomenclature of the areas of the brain is taken from Herrick ('24, '27, '33).

In comparing these blood vessels with those of higher vertebrates, some peculiarities of endocranial anatomy of urodeles should be borne in mind: 1) The morphological simplicity of the brain and its membranes. 2) The extensive development of all of the chorioid plexuses. 3) The presence of a complex nodus vasculosus (of Ecker, Wiedersheim, Gaupp) associated with a massive paraphysis and extensive dorsal sac between the posterior poles of the cerebral hemispheres. 4) The extraordinary size and complexity of the saccus endolymphaticus which envelops the dorsal and lateral aspects of the medulla oblongata and midbrain (figs. 10, 12).

In the figures the outlines of the brain were drawn from dissections of three specimens which were fixed in 10 per cent formalin for 6 weeks. The distribution of arteries and veins, with the exception of the rete over the fourth ventricle in figure 10, which is drawn from a single specimen, has been assembled from sketches of the various specimens studied. The outlines of the median sagittal sections shown in figures 6 and 11 are taken from a drawing by Professor Herrick ('24, fig. 2).

The writer desires to acknowledge his indebtedness to Prof. C. Judson Herrick, under whose direction the work was undertaken, for helpful criticism and encouragement, and for the use of specimens from his extensive collection of microscopic preparations. I am also indebted to Profs. R. R. Bensley and G. W. Bartelmez, and others of the faculty for their kind advice and assistance in matters of technical procedure, and es-

pecially to my friend, Mr. M. H. Knisely, for the use of the apparatus for quartz-rod illumination and for his skillful assistance in its manipulation (Knisely, '34). The illustrations were faithfully drawn from the dissections by Miss Agnes Nixon.

Literature. The most important reports upon the endocranial blood vessels of urodeles are those of Rex (1892), who describes the veins of Triton and Salamandra; Hofmann ('00), whose comprehensive survey includes a brief and very incomplete description of the endocranial arteries of Salamandra; and Osawa ('02), whose monograph on *Cryptobranchus japonicus* includes a good account of the blood vessels of the head, but nothing on the endocranial veins and a very incomplete description of the endocranial arteries.

The other papers cited in the bibliography contribute little to our knowledge of endocranial blood vessels of urodeles beyond what is reported in the three works just mentioned. Warren ('05) recognized the sinusoidal circulation in the paraphysis. Kappers' description ('33) of the endocranial circulation in the vertebrate classes throws light on their phylogenetic relationships, but the urodeles are not mentioned. Dempster's account ('30) of the amphibian endolymphatic organ, its structure and relations to meninges, is essential to an understanding of the endocranial circulation of blood. The work of Gilmore and Figge ('29) describes the transformation of the heart and aortic arches of *Amblystoma tigrinum* during metamorphosis.

ENDOCRANIAL ARTERIES

For preliminary orientation reference may be made to figure 1, a diagram of the chief endocranial arteries seen as projected upon the horizontal plane, and to figure 12, which shows the arrangement of the large veins above the dorsal surface of the brain and their efferent discharge through the jugular sinus.

The endocranial blood supply is from two sources, the cerebral carotid arteries and the basilar artery (fig. 1). The internal carotid artery, as in the frog, breaks up into the

ABBREVIATIONS FOR ALL FIGURES

All figures are of adult *Amblystoma tigrinum*

a.a., arteria auditiva	p.hip., primordium hippocampi
a.b., arteria basilaris	p.p.d., primordium pallii dorsalis
a.c.c., arteria carotis cerebialis	p.pir., primordium piriforme
a.c.c.a., arteria carotis cerebialis, ramus anterior	p.v.hyth., pars ventralis hypothalami
a.c.c.p., arteria carotis cerebialis, ramus posterior	p.v.th., pars ventralis thalami
a.c.i., arteria carotis interna	ped., pedunculus cerebri
a.ch., arteria chorioidea	pl.c.d., plexus chorioideus diencephali
a.ch.d., chorioid artery to diencephalic plexus	pl.c.l., plexus chorioideus lateralis
a.ch.l., chorioid artery to lateral plexus	pl.c.v.q., plexus chorioideus ventriculi quarti
a.o., arteria ophthalmica	r.c.e.b., ramus communicans cum a. basilari
a.pal., arteria palatina	r.c.p., ramus communicans posterior
a.s.a., arteria spinalis anterior	r.h., ramus hypothalamicus
a.s.l., arteria spinalis 1	r.h.m., ramus hemisphaerii medialis
a.s.l.r.a., arteria spinalis 1, ramus anterior	r.h.p., ramus hemisphaerii posterior
a.s.l.r.p., arteria spinalis 1, ramus posterior	r.h.v., ramus hemisphaerii ventralis
b.o.h., branch to opposite hemisphere	r.mes.s., ramus mesencephali superior
b.ol., bulbus olfactorius	r.s.e., rete sacci endolymphatici
cb., cerebellum	r.v.v.q., rete venosum ventriculi quarti
ch., chiasma opticum	s.e., saccus endolymphaticus
com.ant., commissure anterior	s.j., sinus jugularis
com.post., commissura posterior	s.o., sinus obliquus
d.c.n., capillary net of dural tissue	sepf., septal field
epithal., epithalamus	st.amg.f., strio-amygdaloid field
F., foramen interventriculare	tect., tectum
hab., habenula	teg., tegmentum
hyp.g., hypophysis, pars glandularis	v.b.a., vena basilaris anterior
hyth., hypothalamus	v.b.p., vena basilaris posterior
n.c.n., capillary net of nervous tissue	v.d.l.m., vena lateralis medialis durae
nod.vas., nodus vasculosus	v.d.m., vena medialis durae
nuc.ol.ant., nucleus olfactorius anterior	v.h., vena hypothalamica
nuc.ol.d.l., nucleus olfactorius dorso-lateralis	v.h.d., vena hemisphaerii dorsalis
nuc.po., nucleus preopticus	v.h.p., vena hemisphaerii posterior
nuc.tub.p., nucleus tuberculi posterioris	v.h.v.m., vena hemisphaerii ventromedialis
p., paraphysis	v.mes., vena mesencephali
p.d.th., pars dorsalis thalami	v.pros.l., vena prosencephali lateralis
	v.t., vena terminalis
	I. to XII., roots of the cranial nerves

palatine, ophthalmic, and cerebral carotid. The cerebral carotid artery enters the cranial cavity through the carotid canal which lies between the posterior lateral edge of the parasphenoid bone and the lateral process of the occipital

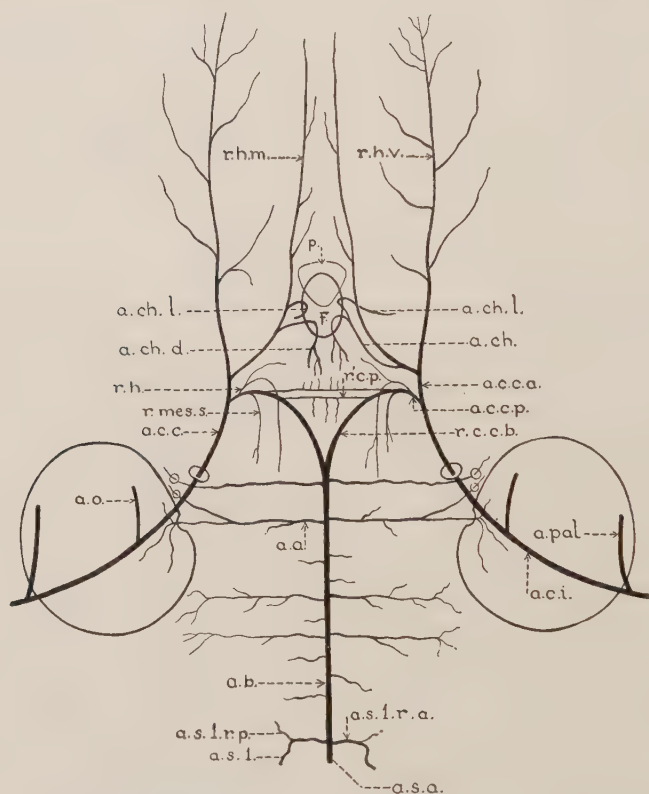


Fig.1 Diagram illustrating the endocranial arterial circulation of *Amblystoma tigrinum* as projected upon the horizontal plane. The paraphysis (p.) is outlined above the interventricular foramen (F.). The ear capsules are sketched for orientation. Not drawn to scale.

bone, this foramen being opposite the distal portion of the hypophysis. The ophthalmic artery separates, in most cases, externally of the foramen, but occasionally endocranially. In the former case it passes forward to the optic nerve which it accompanies into the orbit; in the latter case it emerges from

the cranial cavity through its own foramen and gives off no branches within the cranium. After a short endocranial course the cerebral carotid artery divides into an anterior and a posterior ramus. The posterior ramus, after giving off several branches as described below, becomes continuous with the basilar artery.

Arteria basilaris

The basilar artery (figs. 1, 3, a.b.) enters the cranial cavity in a medioventral position by way of the foramen magnum. This is a continuation of the ventral spinal artery. The arbitrary division of these two arteries may be placed at the superficial origin of the first spinal nerve, where a large artery accompanies the nerve, uniting with the basilar artery. From this point forward the basilar artery lies in a median position on the medulla oblongata, which it supplies. Posteriorly, the ventral spinal artery is supplied by segmental arteries accompanying spinal nerves which enter through the corresponding intervertebral foramina. Each segmental artery divides immediately in the vertebral canal into a ventral and a dorsal ramus and gives off small branches to the dura of the spinal cord. The ventral branch enters the anterior spinal artery and the dorsal ramus the posterior spinal artery. In many cases the posterior spinal artery is nothing more than a slender anastomotic chain of small elongated loops. The ventral spinal artery, however, is a more definite vessel, holding the median position, though frequently there are found stretches of elongated loops.

The first spinal artery (figs. 1, 3, 4, a.s.1.) sends a large posterior ramus dorsally where it bifurcates on the dorso-lateral surface in the region of the calamus scriptorius. The rostral division of this bifurcation supplies the posterior portion of the medulla above the roots of the IX and X nerves. Some of the smaller twigs of this branch run over the edge of the rhomboid fossa extending into the floor of the same (fig. 5). The caudal limb of the bifurcation extends over the dorsal and lateral surfaces of the first few millimeters of the spinal

cord; the most posterior small branches of this limb connect with the dorsal spinal artery. Both the anterior and posterior rami of the first spinal artery give branches to the dura over the medulla.

The basilar artery may take one of two courses after it enters the cranial cavity. It may run as a single vessel almost the entire length of the medulla oblongata, or it may divide almost immediately at the foramen magnum and extend anteriorly as two vessels, each lying lateral to the midline. In the first case the single basilar artery divides in the isthmus region to form the two communicating arteries (fig. 1, r.c.c.b.) from the posterior rami of the cerebral carotid arteries. In the second case, where the basilar artery divides near the foramen magnum, there are usually small anastomoses between the two vessels. In some instances the connecting links between the two divisions of the basilar artery are of large caliber and far apart.

Arteria auditiva. The branches of the basilar artery are numerous and variable. There is one constant branch which is easily recognized by its course and termination. This is the arteria auditiva (figs. 1, 3, a.a.). This artery arises from the basilar at right angles immediately opposite the roots of the VIII nerve. It gives several branches to the ventral surface of the medulla and roots of the VII and VIII nerves. It then sends a small branch into the auditory capsule. There is also a small branch which accompanies the VII nerve through its foramen, and still other fine branches pass over the dorso-lateral edge of the rhomboid fossa and into its floor (fig. 5).

Figure 2 shows an abnormality found in one specimen which may be explained by the failure of the basilar to unite with the communicating artery of one side. There was no visible connection between the two communicating arteries or between the auditory artery on the right side with the basilar artery.

Farther rostrally another large artery leaves the basilar to supply the most anterior portion of the medulla oblongata on all surfaces. It sends small branches to the roots of the

trigeminus nerve, one of which passes through the foramen accompanying the nerve. This artery has small twigs extending into the edge and floor of the fourth ventricle. Occasionally two smaller arteries were found instead of the large one.

At the level of the IX and X nerves the basilar artery gives off one or two branches which supply the area adjacent to the roots of these nerves. Besides the larger branches just

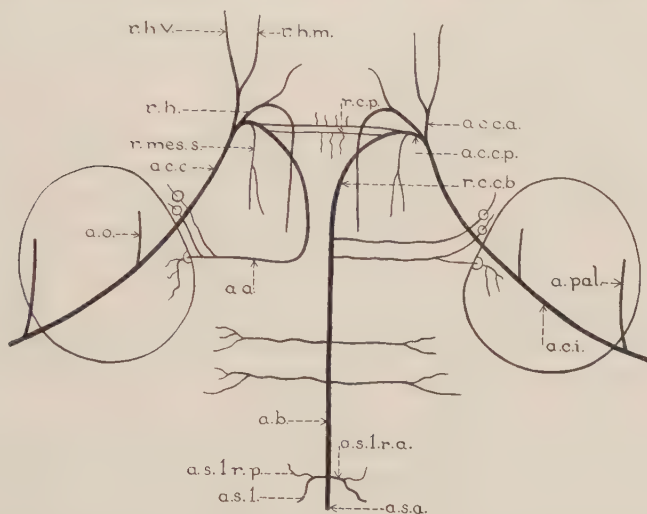


Fig. 2 Diagram illustrating an anomaly. As shown on the left side, the artery normally connecting the posterior cerebral carotid with the basilar (r.c.c.b. of the right side) does not make connection with the basilar, but is continued as the auditory artery (a.a.).

enumerated, there are many smaller ones with no constant or characteristic courses. They supply chiefly the ventral surface of the medulla oblongata. All of these branches of the basilar artery are so extremely variable in origin and course that detailed description seems unnecessary.

The chorioid plexus of the fourth ventricle has a double vascular supply, arterial and venous. Some of the branches of the basilar artery which supply blood to the medulla oblongata from its pial surface continue dorsally to pass over

the edge of the rhomboid fossa. Some of these vessels, after penetrating the taenia of the fourth ventricle, turn ventrally to supply the floor of the ventricle; others turn dorsally as chorioid arteries to enter the chorioid plexus (fig. 12, a.ch.v.q.). The venous supply of the plexus comes from the sinusoidal rete of the saccus endolymphaticus (r.s.e.), which sends vessels downward to penetrate the dura and then subdivide into smaller sinusoidal loops within the lobules of the plexus of the fourth ventricle (r.v.v.q.). The arterial capillary blood drains into the efferent side of these loops, which pass through the dura to enter again the rete of the saccus which is drained by the jugular sinus (s.j.).

In the frog, the vertebral artery has its origin from the arteria occipito-vertebralis, the third branch of the aortic loop. This occipito-vertebral breaks up into the occipital and the dorsal vertebral arteries. From the dorsal vertebral artery a cranial ramus gives rise to the communicating branch with the basilar in the region of the union of the first vertebra with the skull. The dorsal vertebral artery supplies segmental branches to the ventral and dorsal spinal arteries.

In the tiger salamander the dorsal aorta gives rise to segmental branches; a small ramus from each branch penetrates the vertebral canal and divides into dorsal and ventral rami which enter the posterior and anterior spinal arteries, respectively. The first segmental branch of the dorsal aorta (a.s.1.) is large and enters the vertebral canal with first spinal nerve. This artery is comparable with the vertebral of the frog.

Beddard ('05), in a summary of the cerebral arteries in the Lacertilia, states that "the entrance of the vertebral arteries into the anterior spinal marks the end of the medulla." In the tiger salamander, I find, as did Dendy ('09) for *Sphenodon*, that the entrance of the first spinal artery, using Hofmann's term, marks the end of the medulla oblongata. Hofmann speaks of the anterior spinal artery as the tractus spinalis ventralis and the posterior spinal artery as the tractus spinalis dorsalis throughout the whole vertebrate series.

Arteria carotis cerebialis, ramus posterior

The cerebral carotid artery (figs. 1, 3, 4, a.c.c.) divides at the level of the posterior pole of the hemispheres into two vessels, ramus anterior and ramus posterior. These rami are short and within 3 to 5 mm. break up into their respective branches. The posterior ramus divides immediately into the following arteries: 1) r. hypothalamicus, 2) r. mesencephali superior, 3) r. communicans posterior, 4) r. communicans cum a. basilari.

Ramus hypothalamicus. This originates about 2 mm. from the origin of the posterior ramus and spreads ventrally over the lateral and ventral surfaces of the hypothalamus (figs. 3, 4, r.h.). It divides into a short anterior and a more extended posterior division. The anterior division supplies the region about the decussation of the optic nerves. The posterior division supplies the hypothalamus, extending into the glandular portion of the hypophysis, to which it gives an abundant blood supply, breaking up into a close net of capillaries. In the region of the membranous floor of the infundibulum this posterior division breaks up into an extremely fine mesh of capillaries.

In the frog this artery is a branch of the anterior division of the cerebral carotid artery. The name given to it by Ecker-Wiedersheim-Gaupp is rami to the lobus infundibularis. In Sphenodon, Dendy ('09) speaks of it as the arteria infundibularis.

Ramus mesencephali superior. This ramus supplies the dorsal and lateral aspects of the tectum as well as most of the habenular region. Many small branches of its anterior twig penetrate the thalamic region laterally. The artery breaks up into very fine branches, distributed quite uniformly over the optic lobe (figs. 4, 5, r.mes.s.). The most posterior lateral branch passes over to the dorsal surface of the cerebellum as it does in the frog. In addition the cerebellum may also be supplied by a small branch from the basilar artery which comes up from a ventrolateral position, swinging over the lateral aspect of the cerebellum just above the trigeminus

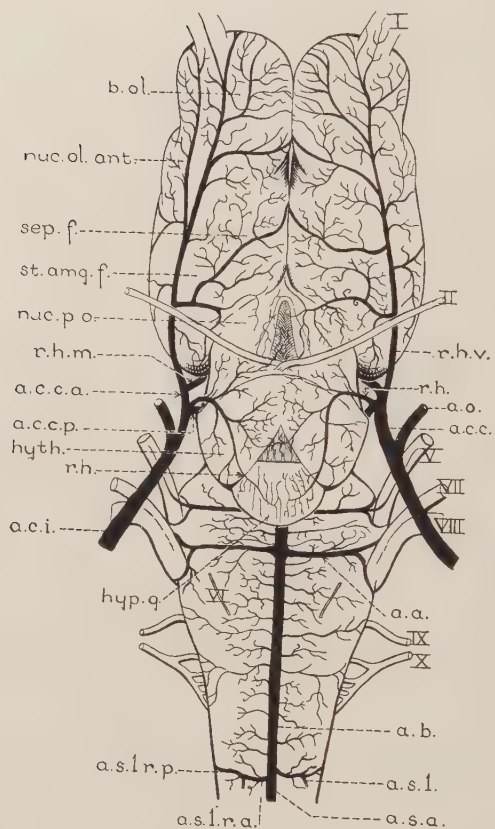


Fig. 3 Ventral surface of the brain, showing the arteries. $\times 7.5$.

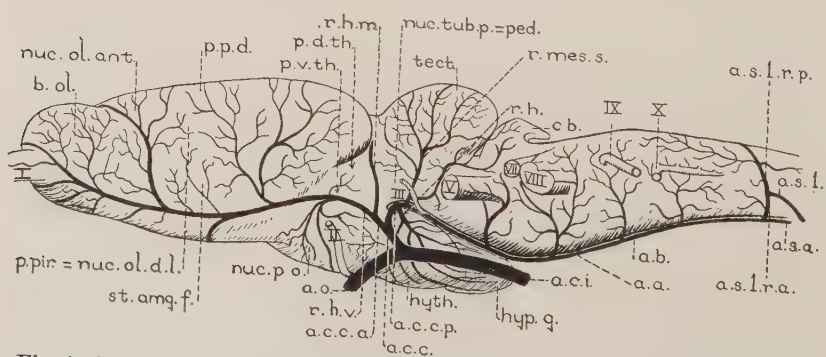


Fig. 4 Left lateral view of the brain and its arteries. The endocranial origin of the ophthalmic artery is here illustrated. $\times 7.5$.

nerve. The distribution of this artery resembles closely that of the frog.

Ramus communicans posterior. This artery is the connecting link between the two cerebral carotid arteries (fig. 1,

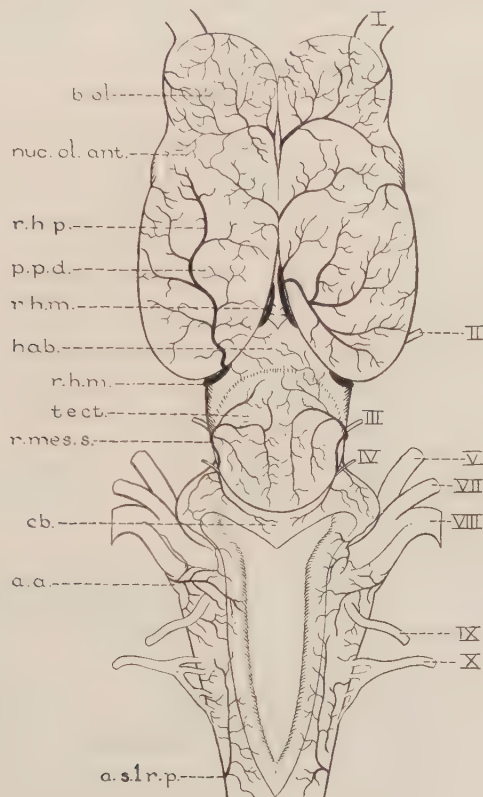


Fig. 5 Dorsal surface of the brain, illustrating the arterial blood supply. The paraphysis, saccus endolymphaticus, and chorioid plexus of the fourth ventricle have been removed. $\times 7.5$.

r.c.p.). It may be either single or double. In either case it arises from the posterior division of the cerebral carotid in common with the artery that communicates with the basilar. There are three or four stubby branches of the posterior communicating artery which penetrate the posterior perforated space dorsally of it. Where there are two communicating

arteries, these perforating arteries generally come from the anterior artery. The dorsal surface of the pars libera of the hypothalamus is supplied by small branches which arise from the posterior communicating artery. These extend as far as the glandular portion of the hypophysis, where they anastomose with the capillary net of this gland. It is the posterior communicating artery which closes the circle of Willis posteriorly (fig. 1).

Ramus communicans cum a. basilari. This artery, as already described, is the fourth branch of the posterior ramus of the cerebral carotid artery (fig. 1, r.c.c.b.).

Arteria carotis cerebialis, ramus anterior

The ramus anterior (a.c.c.a.) immediately divides into two arteries, the ramus hemisphaerii medialis and the ramus hemisphaerii ventralis. These arteries supply the two hemispheres and the dura surrounding them.

Ramus hemisphaerii ventralis. The ventrolateral artery of the hemisphere extends the full length of the forebrain on its ventrolateral aspect (figs. 3, 4, r.h.v.). There is some variation of the left and right arteries. Generally the right divides and the divisions run parallel to each other. In rare cases the left may do likewise. In about one-third of the specimens both arteries were single. Both arteries give off small irregular branches to the dura on the ventral surface which then swing laterally and anteriorly to the dorsal surface.

In addition to supplying the ventrolateral surface, this artery extends branches directed ventromedially to the lower third of the medial aspect of the hemisphere. There is variation in the number of these branches, both in the hemispheres of the same individual and in those of different individuals. There are usually three or four. Figure 3 illustrates three branches on the right hemisphere and four on the left. The two anterior branches are most constant. As illustrated, the most caudal branches, two on the left and the large one on the right, supply corresponding areas in their respective hemispheres. These areas are the preoptic and septal nuclei.

The two anterior medially directed branches supply large areas which include the anterior olfactory nucleus and bulb on the ventral and lower thirds of their medial surfaces. The ventral hemispherical artery breaks up into many very small branches which supply the olfactory bulb on all surfaces except the dorsal.

The olfactory nerve receives fine branches which have their origin from the anterolateral and ventral branches of the ventral artery on the olfactory bulb. These olfactory branches extend as far as the nasal capsule, where they anastomose with the terminal branches of the palatine artery in the mucous layer. In a good preparation and with proper illumination it is possible in the living animal to see these arteries of the olfactory nerve deeply embedded in the nerve itself. Careful observation of the blood flow indicates a uniform distribution of these fine arteries. From these anterior branches of the ventral hemispherical arteries many small branches swing over into the dura and these give rise to the dural veins on the dorsal and lateral areas of the hemispheres as described later.

The piriform and striatal fields are supplied by a large vessel which has its origin from the ventral hemispherical artery in the proximal third of its course. This branch runs laterally and then dorsally over these fields. As shown in figures 3 and 4, another ventrolateral branch of this artery also supplies, in some cases, the anterior portions of the above-mentioned areas, the lateral surfaces of the anterior olfactory nucleus and the posterior portion of the olfactory bulb.

Ramus hemisphaerii medialis. This artery passes from its origin almost directly dorsalward at the level of the posterior pole of the hemisphere (figs. 1, 3, 4, 5, 6, 7, 12, r.h.m.). It then turns anteriorly in the stem-hemisphere fissure between the posterior pole of the hemisphere and the diencephalon. It supplies the dorsal two-thirds of the medial surface of the hemisphere (fig. 6), most of the dorsal surface (fig. 5), and the diencephalic and telencephalic chorioid plexuses.

Ramus hemisphaerii posterior. Near the origin of the medial ramus under the posterior pole of the hemisphere

there is a large branch which spreads over the posterior pole, then forward on the dorsal surface. This may be called the *ramus hemisphaerii posterior* (fig. 5, r.h.p.). This hemispherical artery may be small and limited in distribution to the posterior pole, in which case the posterior half of the dorsal pallial area is supplied by branches of the medial artery which arise in the vicinity of the paraphysis, as shown on the right side of figure 5.

The chorioid arteries, as described beyond, have variable origins within the stem-hemisphere fissure or farther forward in the vicinity of the paraphysis. Rostrally of the paraphysis in most specimens there are two large branches of the medial

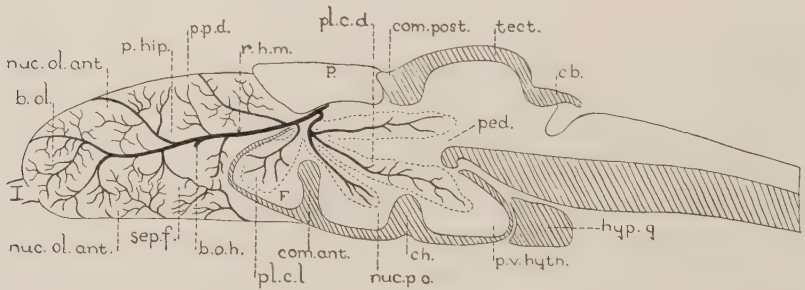


Fig. 6 Median sagittal section of the brain, illustrating the course of the medial hemispherical artery and (very schematically) the chorioid arteries. Cut surfaces of the massive wall of the brain are cross-hatched. The lower portion of the paraphysis has been removed. $\times 7.5$.

artery which supply the primordium hippocampi, the rostral part of the dorsal pallial area, and the medial and dorsal parts of the anterior olfactory nucleus and olfactory bulb (figs. 5 and 6). Other small branches of the main trunk of the medial artery descend to enter the septal field. At the rostral end of the hemisphere the medial artery breaks up to participate in the dense arteriovenous plexus which envelops the olfactory bulbs and anterior olfactory nucleus. This superficial plexus also penetrates into the interior of the olfactory bulb and anterior olfactory nucleus, where, in addition to a very rich capillary net, there are direct anastomoses between arterioles and venules. The vascular pattern of this region is complex and variable.

There is in some cases a vicarious relation between the medial arteries of the two sides. If the artery of one side is weak, the artery of the opposite side sends a compensating branch across to supply the lack (figs. 6, 7, b.o.h.). There is no anastomosis between the two medial arteries, for the branch which crosses the median fissure penetrates the tissue of the opposite hemisphere. Neither here nor elsewhere do we find evidence of a closure of the circle of Willis anteriorly.

Arteriae chorioideae. The arteries which in the aggregate supply the diencephalic and telencephalic chorioid plexuses may be called chorioid arteries. In origin and course they are extremely variable and they are rarely even approximately symmetrical on the two sides of a specimen. Several arrangements of chorioid arteries will be described, but no one of these occurs with sufficient constancy to be called typical.

In some cases a branch separates from the medial hemispherical artery near the posterior pole of the hemisphere and runs parallel with the main artery in the floor of the stem-hemisphere fissure to the level of the nodus vasculosus (figs. 1, 7, right side, a.ch.). Here it penetrates the paraphysis, within which it breaks up into several divisions which are distributed to the diencephalic and telencephalic chorioid plexuses.

In other cases, and frequently on the side opposite the arrangement just described, the dorsomedial artery passes without division through the stem-hemisphere fissure to reach the medial wall of the hemisphere. Here at some point opposite the paraphysis it gives one or two large branches which turn inward to ramify within the chorioid plexuses (figs. 1, 7, left side). All of the chorioid arteries may arise from a common stem, or the lateral chorioid artery (a.ch.l.) may arise from the medial ramus independently of the arteries for the diencephalic plexuses (a.ch.d.).

These arrangements of the chorioid arteries have been seen in dissections of injected specimens, in microscopic sections, and by transillumination of the living animal. As seen in the living specimen under quartz-rod illumination, the chorioid arteries penetrate the paraphysis, within which they branch

more or less. There is further subdivision in the roots of the chorioid plexuses. An arterial trunk extends the entire length of each lobule of the plexus, accompanying the large venous sinusoids that course in the loose meningeal tissue of the interlobular spaces. Small arterioles ramify throughout all lobules and at their margins break up into a complex and close-meshed capillary net. From this capillary bed venules are assembled which discharge into the big venous sinusoids.

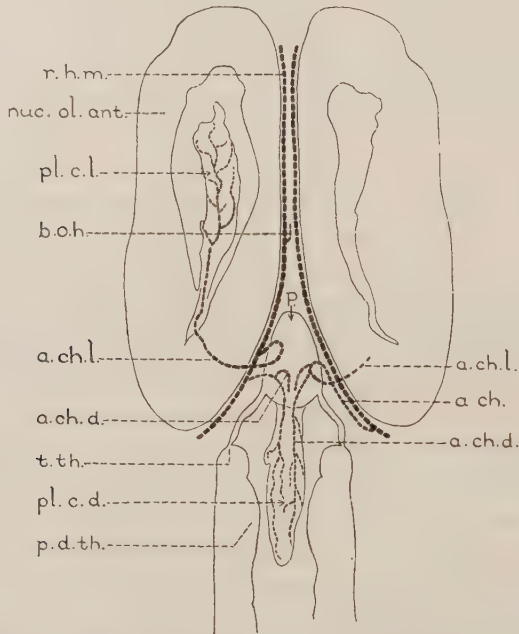


Fig. 7 Diagram illustrating the courses of the chorioid arteries of the diencephalic and telencephalic plexuses as seen in a dissection from the dorsal side.

Quantitative pattern of arterial blood supply

From the preceding description it is evident that the nervous tissues of the brain and the chorioid plexuses have an arterial supply which breaks up into a capillary net comparable with that of the systemic circulation in other parts of the body. The curious simple capillary loops and arteriovenous anastomoses described by Schöbl (1882) do not

exist in our specimens, and his account was probably based on poorly preserved material.

Rough, graphic reconstructions of the arteriole-capillary-venule complex reveal a very irregular and contorted arrangement. The capillaries, it is true, are very large and in some cases it is difficult to see where arterioles leave off and capillaries begin, but continuous observation of the flowing blood in the living animal reveals this difference. In most cases the capillary loop is coiled even more than the arteriole, while the venule tends to straighten out into a larger channel. The capillary net pictured in the anterior olfactory nucleus in figure 12 (n.c.n.) shows diagrammatically this relationship, which is true for other areas with the exception of slight differences in density. Also, roughly speaking, each separate area has its own peculiar pattern of vascular arrangement. A good example of this is in the glomeruli of the olfactory bulb, where each glomerulus receives a richer capillary net.

The relative distribution of the vascular density in the various areas of the brain, exclusive of dural vessels, may be summarized as follows: The olfactory bulb and the anterior olfactory nucleus immediately adjacent to it receive the richest blood supply as compared with other areas of the hemisphere. The ventral or subpallial areas have a richer vascular supply than the dorsal or pallial areas. The more medial portions on the ventral surface appear to receive more arterial twigs than the more lateral. This means that the septal nuclei and the more medial areas of the strio-amygdaloid field are richer proportionately than the more lateral and dorsal portions of the hemisphere. In comparing the medial and lateral surfaces of the hemispheres, the medial field is richer in arterial distribution, with the exception of the olfactory bulbs where the supply is uniform on both surfaces.

The optic tectum is richly supplied by the superior mesencephalic artery and seems to be slightly more vascular than the olfactory regions. The thalamus is the richest of all parts of the brain, even more so than the olfactory bulbs. The differences in vascularity between the various areas of the

medulla oblongata are very small. The dorsolateral regions are slightly more vascular than the ventromedial, and the relative capillary density of the medulla oblongata as a whole is slightly less than that of the hypothalamic region.

These statements are not based upon exact measurements, but on observations under the dissecting microscope and microscopic sections. These are conclusions based upon comparisons of mental pictures retained from one observation to another and by placing two injected specimens side by side. In two or three instances it was possible to shift two or three live specimens under the microscope for comparison, not only for checking various areas on the same individual, but the same and different areas on separate animals. Such estimates are not valid quantitatively, but represent judgments subject to errors of observation.

ENDOCRANIAL VEINS

The most interesting features of the vascularity of the brain of *Amblystoma* are found in the venous return. The veins all discharge through the rete of the nodus vasculosus or the rete of the saccus endolymphaticus or both, so that the relations of these parts must first be described.

Paraphysis, dorsal sac, and nodus vasculosus

The rete of the nodus vasculosus permeates the paraphysis and dorsal sac and is in free communication by wide sinusoids with the venous channels of the diencephalic and telencephalic chorioid plexuses.

As described by Warren ('05), the embryonic velum transversum of urodeles gives rise by evagination to the dorsal sac on the diencephalic side and to the paraphysis on the telencephalic side. In adult *Amblystoma* the fusion of these two structures and the development within them of a dense rete of venous sinusoids produces the structure which Gaupp terms the nodus vasculosus in the frog. This rete of *Amblystoma* receives nearly all of the efferent blood vessels from both cerebral hemispheres. This blood is discharged backward

through the oblique sinuses into a similar rete of the saccus endolymphaticus and chorioid plexus of the fourth ventricle. These sinusoids and the related veins form a closed vascular system of extraordinary complexity. The walls of all of these vessels, except the larger veins (but not excepting the sinusoids), are very thin.

The veins from the cerebral hemispheres, except their posterior parts, and from the overlying dura enter the nodus vasculosus in three systems: 1) a dorsal system of dural and hemispherical veins (figs. 10, 12), 2) a ventromedial system which enters the paraphysis at its rostroventral angle (fig. 11), and, 3) a system of chorioid vessels which discharge from the chorioid plexuses into the rete of the paraphysis and dorsal sac along its ventral and caudal borders (fig. 11). The oblique sinuses leave the posterior border of the dorsal sac above the epithalamus (figs. 10, 12, s.o.).

The dural veins above the hemispheres may enter the paraphyseal rete, or some of them may pass farther back to enter the oblique sinuses or rete of saccus endolymphaticus. The dorsal hemispherical vein (fig. 10, v.h.d.) enters the paraphyseal rete, within which it may pass directly spinalward into the oblique sinus with only small anastomoses with the sinusoids of the nodus vasculosus. Most specimens, however, show wide anastomoses, as shown in figure 12. The sinusoids of the two sides freely communicate by wide anastomoses within the nodus vasculosus (not shown in fig. 12). Observations on the living animal show two large laterally placed venous channels in the dorsal part of the nodus vasculosus which seem to be collecting vessels for the incoming dorsal veins and also for the outflow through the oblique sinuses.

Saccus endolymphaticus

Dempster ('30) has given a good account of the development and adult structure of the endolymphatic organ of Amblystoma and other Amphibia, to which there is here added a description of the related blood vessels. In adult Amblystoma the lobulated endolymphatic sacs are expanded to cover the

dorsal and lateral aspects of the brain stem from the level of the VIII cranial nerve roots forward to the cerebral hemispheres. In some cases they may extend forward along the lateral aspects of the hemispheres for half their length. The two sacs are broadly united dorsally over the posterior part of the tectum, cerebellum, and anterior part of the medulla oblongata. As Dempster says, they are fused dorsally; but in our specimens preserved shortly after the metamorphosis, though the two sacs are intimately joined and their lobules interdigitate, there is no communication between their cavities. Whether the separating epithelial walls at the plane of junction break down in older specimens has not been determined.

The two endolymphatic sacs envelop the rostral part of the chorioid plexus of the fourth ventricle, from which they are separated by an imperfectly differentiated dural membrane (Dempster, '30, p. 75). This is comparable with the arrangement in the human embryo described by Streeter ('16), and, as will appear beyond, there are striking similarities in the vascular supply of the saccus.

After metamorphosis the endolymphatic sacs are densely filled with masses of calcium carbonate and calcium phosphate in the proportion of 65 per cent carbonate and 27 per cent phosphate. The former are laid down as aragonite and the latter as dahlite. The x-ray and chemical data are given in a note by Dr. A. B. Hastings following this paper, for which we extend our cordial thanks. The lobules of the saccus are pouched outward between the meshes of the large venous sinuses by which this organ is enveloped. The contrast between the pigmented vessels and the glistening white mass of saccus deposits seen through the transparent epithelium of the saccular lobules gives the saccus, or 'chalk sac,' a striking appearance in a dissection (fig. 10).

In midlarval stages each saccus endolymphaticus is a simple slightly lobulated ovoid vesicle enmeshed by a close rete of large blood vessels. Blood is discharged into this rete by the oblique sinuses and other vessels. The larger channels extend from the oblique sinuses spinalward in the medial wall

of the saccus, thence backward and lateralward into the jugular sinus. The two endolymphatic sacs lie nearly in contact dorsally of the chorioid plexus of the fourth ventricle separated by the large venous channels just mentioned, and between these channels of the two sides there are wide anastomoses. The main flow of blood, accordingly, is from the oblique sinuses backward between the endolymphatic sacs, and then outward into the jugular sinuses. But numerous large sinusoidal vessels spread from these main channels in the form of a close-meshed network which completely envelops each saccus (see figure by Herrick, '34).

In later stages, as the saccus enlarges and becomes more intricately lobulated, the ramifications of sinusoids connected with the oblique sinuses and other blood vessels become much more complex and the larger fore-and-aft channels are spread over the medial and dorsal surfaces of the endolymphatic sacs, the whole system forming a close meshwork of big vessels. One oblique sinus is usually much larger than the other, yet the wide anastomoses throughout the common rete of both endolymphatic sacs insure an even distribution of blood.

At the beginning of metamorphosis the two endolymphatic sacs are closely joined dorsally by interdigitation of their lobules, but their cavities do not communicate. The vessels of the chorioid plexus of the fourth ventricle are sparsely pigmented, while those of the saccus carry much pigment. There is a layer of abundant pigment between the two endolymphatic sacs and in the dural membrane between them and the chorioid plexus. There are sinusoidal connections between the rete of the saccus and that of the chorioid plexus of the fourth ventricle. The larger vessels of the dorsal and ventral surfaces of the saccus converge toward its caudolateral border, where they join to form the jugular sinus which leaves the cranial cavity in company with the vagus roots.

Dural veins

The dural veins are not illustrated here, except for the oblique sinus and the median veins of the cerebral hemispheres

shown in figure 12. The drainage of the dura of the spinal cord is chiefly into the ventral spinal vein. Few of the smaller veins of the dura in the region of the upper cord are continuous with those of the medulla oblongata. In the region of the medulla oblongata, ventrally, the dural veins are very irregular in their course and run forward to empty into the rete of the saccus endolymphaticus at its most ventral and posterior tip. There are but few veins in the dura above the medulla posterior to the endolymphatic sac; these run forward into the veins of the saccus.

In the region of the hypothalamus there are long anastomotic vessels between the veins of the hemispheres and those of the rete of the saccus. These pass below the decussation of the optic nerves. Above the optic lobes there are occasional anastomotic loops between the veins of the lateral processes of the saccus and the oblique sinus.

In the dura, ventral to the hemispheres, many small irregular anastomotic loops occur. The drainage of the greater portion of these, especially in the caudal two-thirds, is by laterally placed veins which empty into veins of the extended lateral processes of the saccus endolymphaticus.

The anterior third of the dura on the ventral surface of the forebrain is drained by small veins which run over the medial, anterior, and lateral surfaces of the olfactory bulbs dorsally. These small veins unite to help form three medially placed veins (fig. 12, v.d.m. and v.d.l.m.); one usually remains more or less uniformly in the median position. Its companions, one on either side, have tortuous courses. All three usually enter the nodus vasculosus. In many instances the more laterally placed vessels (v.d.l.m.) may enter the oblique sinus or the rete of the saccus endolymphaticus. There are still two other small veins (not figured) which run the greater length of the hemisphere and lie in a dorso-lateral position in the dura and empty either into the oblique sinus or the rete of the endolymphatic organ. In all instances there are long anastomotic links between these most laterally placed vessels and the companion vessels of the median vein. In a few instances the

most medially placed vessel is omitted, leaving the two other medial vessels (v.d.l.m.) closer together. No median sagittal sinus has been seen, as described for *Triton cristatus* by Rex (1892).

Veins of the brain

The description of the superficial veins of the brain begins at the olfactory bulbs and follows, in general, the course of the blood flow backward to its discharge into the jugular sinuses. This blood is accumulated from the capillary networks of the leptomeninges, walls of the brain, and chorioid plexuses.

The olfactory bulbs are exceedingly vascular and from the capillary net of this region venules pass backward to converge into venous trunks on the ventral, medial, and dorsal surfaces of the brain.

Vena hemisphaerii dorsalis. This vessel spreads over the dorsal and upper lateral surfaces of the olfactory bulb and anterior olfactory nucleus (figs. 10, 12, v.h.d.). It passes backward in a zigzag course, receiving branches from the medio-dorsal part of the hemisphere, to enter the nodus vasculosus at its dorsal border.

Vena hemisphaerii ventromedialis. This name is given to a system of large and exceedingly variable veins which discharge into the rostroventral angle of the paraphyseal rete in the median plane above the interventricular foramen (fig. 11, v.h.v.m.). This blood is derived from the ventral, ventrolateral, and ventromedial walls of both cerebral hemispheres (figs. 8, 9).

The more dorsal trunk receives branches from the medial side of the olfactory bulb and anterior olfactory nucleus and from the primordium hippocampi. The more ventral trunks are distributed in two systems, anterior and posterior (fig. 8). The anterior system spreads over the ventral parts of the olfactory bulb and anterior olfactory nucleus. The posterior system drains the septal and strio-amygdaloid fields and the preoptic nucleus. The veins of both systems converge in the median fissure (fig. 11). Their courses are exceedingly variable. They may enter the rete of the paraphysis and chorioid

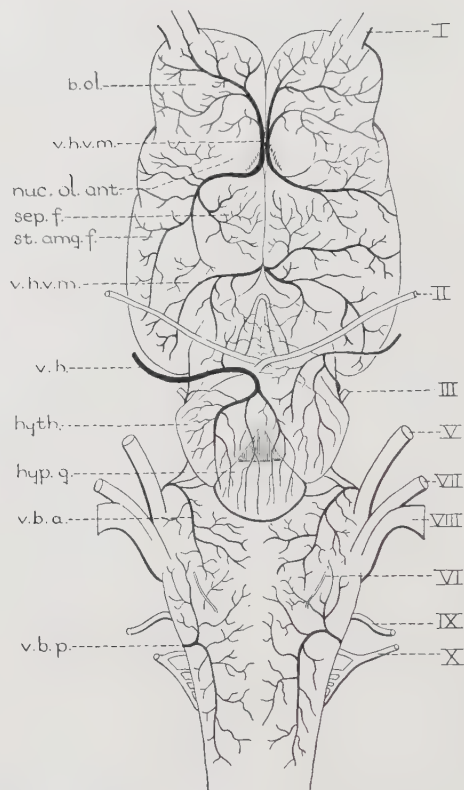


Fig. 8 Ventral surface of the brain, illustrating the veins. $\times 7.5$.

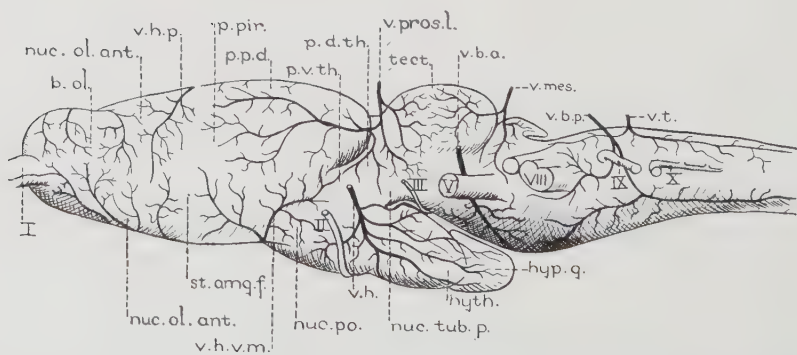


Fig. 9 Left lateral aspect of the brain, showing the arrangement of the pial veins. $\times 7.5$.

plexus in one or several trunks, they may combine wholly or in part with the dorsal median trunk, which may be single or double, and some or all of these veins from both hemispheres may unite to enter the paraphysis in a single large vessel.

The large dorsal and ventromedial veins just described enter the sinusoidal rete of the nodus vasculosus and related chorioid plexuses. All of the blood contained in these vessels is conveyed by wide sinusoidal channels toward the caudal border of the dorsal sac above the epithalamus, and from here into the oblique sinuses.

Venae chorioideae. The telencephalic and diencephalic chorioid plexuses are invaginated from the septum ependymale, the caudoventral border of the paraphysis, and the dorsal sac. The venous channels of these plexuses in the aggregate may be called chorioid veins (fig. 11, v.ch.). They are mostly wide sinusoids in free communication with those of the paraphysis and dorsal sac at the roots of the plexuses.

Venae taeniae. There are small veins formed by converging venules of the posteromedial wall of the hemisphere which cross the taenia thalami and taenia fornicis, enter the nodus vasculosus, and there discharge into the large venous sinusoids. These in the aggregate may be called taenial veins. They have been seen in sections and by transillumination of the living animal, but are not illustrated in the figures.

There is an arterial capillary net in the chorioid plexuses, as previously described, from which collecting venules carry blood into the chorioid sinusoids, thence upward and backward through the sinusoids of the nodus vasculosus to the oblique sinuses. The arrangement of these sinusoids of the plexuses and of their connections with the common rete of the paraphysis and dorsal sac is so variable that no description of a typical pattern can be given.

The veins which remain to be described do not pass into the nodus vasculosus, but converge by various channels into the oblique sinuses or rete of the saccus endolymphaticus. The blood from practically all of the endocranial vessels enters the common sinusoidal rete of the saccus and chorioid plexus of

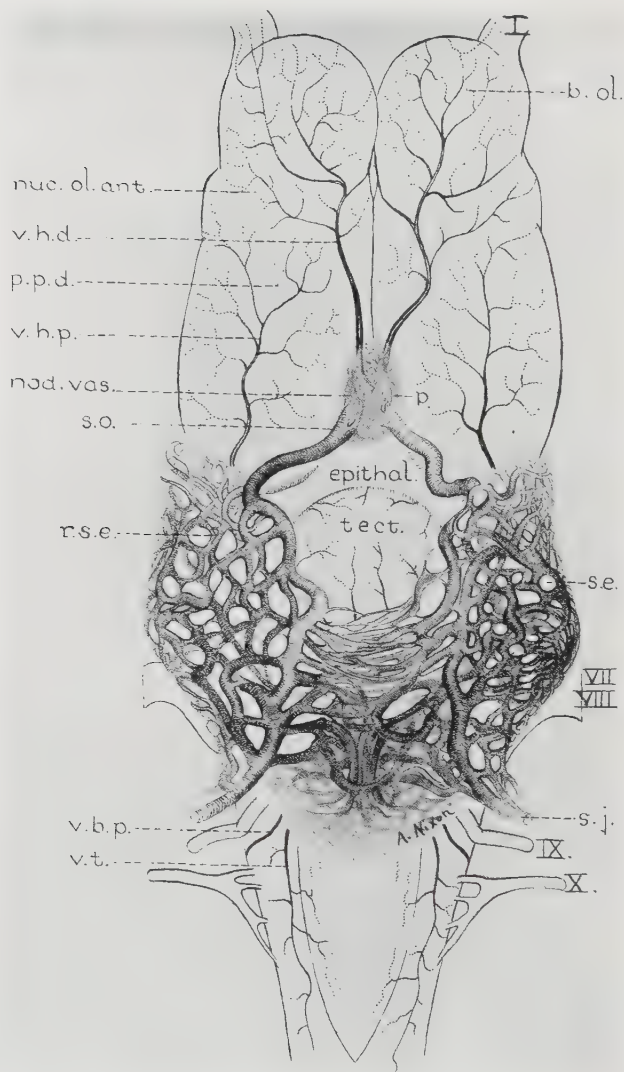


Fig. 10 Dorsal aspect of the brain drawn from a dissection in which the paraphysis and endolymphatic organ are intact, illustrating the convergence of all pial veins into the sinusoids of the paraphysis and saccus endolymphaticus and their common outlet through the jugular sinus. $\times 10$.

the fourth ventricle, which serves as a collector for the final discharge into the jugular sinuses.

Vena hemisphaerii posterior. This vessel drains most of the dorsal pallium, extending forward to reach variable amounts of the lateral part of the anterior olfactory nucleus and rostral part of the piriform area (figs. 9, 10, 12, v.h.p.). It may discharge either into the oblique sinus or farther back into the rete of the saccus endolymphaticus.

Vena prosencephali lateralis. This vein receives blood from most of the piriform area, the upper border of the somatic striatum, epithalamus, thalamus, cerebral peduncle, and the anterior third of the optic tectum (fig. 9, v.pros.l.). The

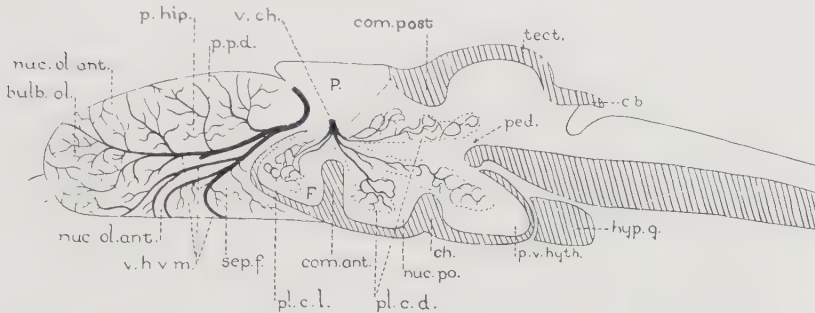


Fig. 11 Median sagittal section of the brain, showing the veins of the medial wall of the hemisphere and (more diagrammatically) those of the chorioid plexuses. $\times 7.5$.

short trunk formed by the union of all of these branches enters the rete of the endolymphatic sac.

Vena mesencephali. This is the chief outlet of blood from the posterior two-thirds of the optic tectum and cerebellum (fig. 9, v.mes.). The stem formed by union of these two branches passes dorsally into the endolymphatic rete.

Vena hypothalamica. This large vein drains the posterior part of the preoptic nucleus and the entire hypothalamus, including the hypophysis (figs. 8, 9, v.h.). Its main trunk passes dorsally parallel with the optic tract to enter the rostral part of the endolymphatic rete. In one specimen there was seen a large arterio-venous anastomosis between this vein and the hypothalamic artery.

Vena basilaris anterior. The drainage area of this vein includes the ventral and ventrolateral parts of the brain stem between the roots of the III and VIII cranial nerves (figs. 8, 9, v.b.a.). It passes dorsalward in front of the V nerve roots to enter the rete of the endolymphatic sac.

Vena basilaris posterior. This vein drains the ventral and ventrolateral parts of the medulla oblongata from the roots of the VII nerve spinalward. The more rostral branches spread over the lateral surface dorsally and ventrally of the VIII roots (figs. 8, 9, v.b.p.). Its most caudal branches anastomose with the venous loops of the ventral surface of the upper spinal cord. The main trunk passes dorsally behind the roots of the IX nerve to enter the endolymphatic rete.

Vena terminalis. This is the vein of the dorsal and dorsolateral areas of the medulla oblongata (figs. 9, 10, v.t.). Lateral branches extend downward to the level of the VIII, IX, and X nerve roots and medial branches pass over the rhomboidal lip into the floor of the fourth ventricle. Its most caudal branches anastomose with the dorsal spinal vein. It discharges into the caudal part of the endolymphatic rete above roots of the IX nerve.

Sinus obliquus. These big vessels, passing in and under the dural membrane, form the main channels for flow of blood from the nodus vasculosus to the rete of the saccus endolymphaticus and chorioid plexus of the fourth ventricle (figs. 10, 12, s.o.). In size and course they are extremely variable, and there is usually pronounced asymmetry. Often practically all of the blood flow is carried by the right or left sinus; in this case the dominant vessel may lie nearly or quite in the midplane above the tectum instead of across its dorsolateral aspect as usual.

The relations of the oblique sinuses and other veins to the sinusoidal rete of the saccus endolymphaticus have already been described. There are broad sinusoidal connections through the dura between this rete and that of the chorioid plexus of the fourth ventricle. The efferent veins from the plexus go out laterally to connect with the lateral sinusoids of

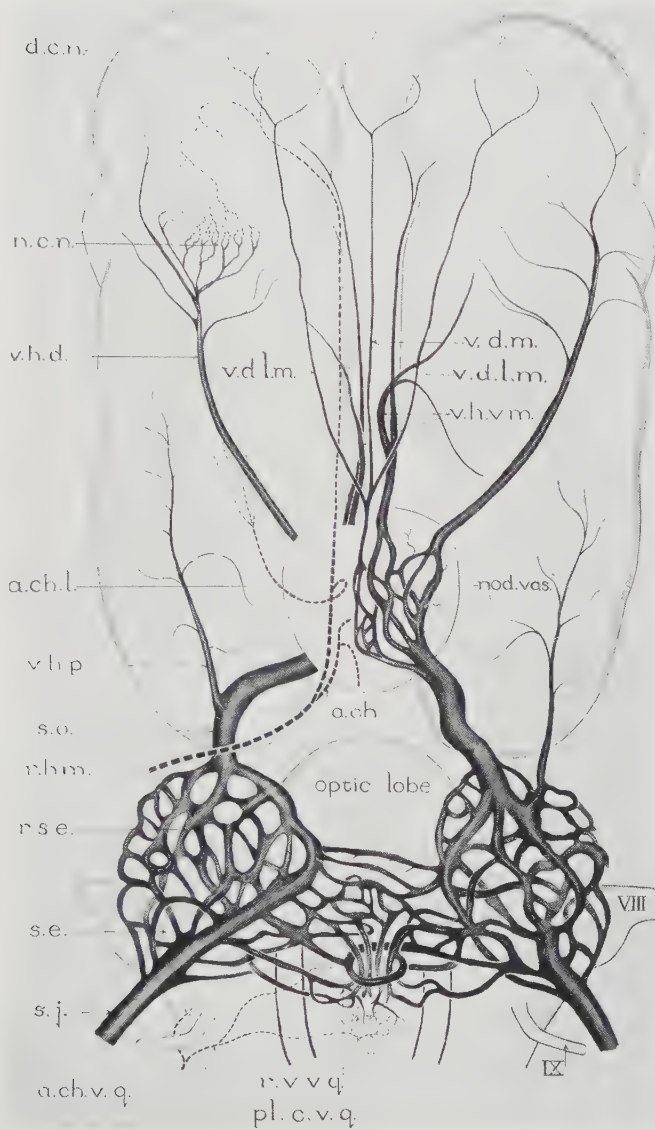


Fig.12 Diagram to illustrate the chief channels of venous return from the brain. The course of the left medial hemispherical artery and the origin of the chorioid arteries from it are indicated in broken lines. Only the three more medial dural veins are drawn. The larger sinusoidal channels of the nodus vasculosus are drawn on the right side; their wide anastomoses with those of the left side are not shown. Not drawn to scale.

the saccus endolymphaticus and thence into the jugular sinuses. Observations on the living animal show that the big sinusoids between the endolymphatic sacs and the medial part of the chorioid plexus (fig. 12, r.v.v.q.) carry blood from the saccus to the plexus and that there is no reverse flow through them from the plexus to the saccus. The efferent drainage from the chorioid plexus by its lateral veins carries blood derived both from the saccus and from the intrinsic arterial capillary net of the plexus.

Sinus jugularis. Enormous sinusoids of the posterolateral border of the endolymphatic sac unite to form the jugular sinus (figs. 10, 12, s.j.), which leaves the cranial cavity through the jugular foramen in company with the roots of the IX and X cranial nerves to join the internal jugular vein.

There are minor outlets from the rete of the saccus endolymphaticus through the foramina of the trigeminal and facial nerves; these small vessels discharge into the internal jugular vein. In the frog the main drainage of the endocranial vessels is by way of the trigeminal foramen into the internal jugular vein.

DISCUSSION AND SUMMARY

The arterial blood supply of the brain of *Amblystoma* is essentially similar to that of other urodeles so far as these have been described and is comparable in most respects with that of *Anura*. Individual variations in the courses of even the major arteries are surprisingly great, and the courses of the veins are even more erratic.

The larger subdivisions of the brain, in general, do not receive their blood supply from a single artery or integrated system of arteries, and individual variations in the sources from which these areas are vascularized are great. This is true whether these areas are defined morphologically or in terms of their functional specificities. It is probable that the morphological and physiological specificities of these areas are determined before they are vascularized. The morphogenetic agencies which determine the vascular patterns are as yet unknown.

The meninges of the olfactory bulbs and anterior olfactory nucleus contain a very dense entanglement of arteries and veins, with numerous arteriovenous anastomoses, and the internal capillary net of this region is more closely meshed than in most other parts of the brain. These arteries are ramifications of the ventral and medial rami of the anterior division of the cerebral carotid artery. The strio-amygdaloid field is supplied by branches of the ramus hemisphaerii ventralis; most of these branches are rather large and extend beyond this field into the adjoining piriform and septal areas also. The septal field is supplied mainly from the ventral ramus, as just mentioned, but its dorsomedial part receives terminals also from the medial ramus and arterioles from these two trunks frequently anastomose.

The pallial areas show the same lack of specificity in their arterial supply as the subpallial fields. The primordial piriform area, or dorsolateral olfactory nucleus, receives its blood from branches of the ventral ramus of the hemisphere which also supply the strio-amygdaloid field or the anterior olfactory nucleus and olfactory bulb. The primordial hippocampus is wholly supplied by branches of the medial ramus, and most of these branches extend beyond the hippocampal area into the dorsal pallial area also. The dorsal pallium in some cases is supplied almost wholly by branches from the medial ramus of the hemisphere with some supply from the ventral ramus and the posterior ramus (fig. 5, right side). In other cases it is supplied almost wholly by the posterior ramus of the hemisphere with some supply from the medial and ventral rami (fig. 5, left side). The ramus hemisphaerii posterior in some cases is distributed specifically to the posterior pole; in other cases, as just mentioned, it may extend also far forward to spread over almost the whole extent of the dorsal pallial area. The chorioid arteries are always derived from the ramus hemisphaerii medialis.

The thalamus and epithalamus are typically supplied by branches of the ramus mesencephali superior, but more or less of this field may be supplied from other sources. The large

preoptic nucleus is supplied in part by branches of the ventral ramus of the hemisphere and, more posteriorly, by branches of the ramus hypothalamicus. The last mentioned ramus is otherwise specifically distributed to the hypothalamus.

Practically the whole of the midbrain is supplied by the ramus mesencephali superior, which extends backward into the cerebellum. The lateral part of the cerebellum and auricle may receive also branches from the ramus of the basilar artery associated with the trigeminal roots. The medulla oblongata is supplied by branches of the basilar artery which are variable in origin and course and whose distribution does not seem to be correlated with the morphological subdivisions of this part of the brain.

The systemic capillary net in the nervous walls of the brain is relatively simple with wide meshes. Though no quantitative measurements have been made, it is evident from inspection that the density of the capillary meshwork varies in different parts of the brain, as briefly summarized on page 275.

The venous return from the brain has some peculiar features in all Amphibia, and these are accentuated in *Amblystoma*. Throughout the meninges, the massive walls of the brain, and the chorioid plexuses the arterioles break up into a capillary net which discharges into venules as in the systemic circulation of other parts of the body. This venous blood then passes through one or two systems of wide sinusoids, each of which presents the morphological characteristics of an endocranial portal system of blood vessels. All endocranial blood vessels form a closed system in which the blood first passes through typical arteriovenous capillaries, then through a rete of wide sinusoids with very thin walls, and the blood from the cerebral hemispheres passes successively through two such sinusoidal networks, that is, through a double endocranial portal system. Nearly all of this endocranial blood converges into the jugular sinuses, through which it leaves the cranium to enter the jugular veins.

The systemic arteriovenous network shows three intergrading types: 1) In the nervous tissue of the brain the

arterioles and capillaries are tortuous, while the related venules take straighter courses outward into the pial veins (fig. 12, n.c.n.). 2) In the dura arterioles and venules are hardly distinguishable from each other and from the capillaries (fig. 12, d.c.n.). Their limits can be determined by observing the direction of flow of blood in the living animal. 3) In the chorioid plexuses the arteries are relatively straight, the capillaries and venules are extremely tortuous, and the venules discharge into the wide venous sinusoids of the plexus. This can be observed in histological material and more clearly in the living animal by transillumination of the plexus after removal of the dorsal wall of the brain.

After passing through the systemic capillaries, as just described, the collecting veins of the brain stem and the posterodorsal parts of the cerebral hemispheres discharge into the oblique sinuses and through these into the sinusoidal rete of the endolymphatic sacs and chorioid plexus of the fourth ventricle, or directly into this rete. In the cerebral hemispheres there is a further complication, for all of the veins of this region (except those from the posterodorsal parts of the hemispheres) discharge into the sinusoidal rete of the paraphysis, dorsal sac and chorioid plexuses of the third and lateral ventricles. The sinusoids of this rete are very large and densely crowded; they are so interconnected by wide channels as to suggest that this complex rete is a functional unit. All of the blood of this rete is collected at the posterodorsal border of the dorsal sac and discharged backward through the oblique sinuses into the similar rete of the saccus endolymphaticus. The main features of this remarkable arrangement of endocranial veins and sinusoids are illustrated somewhat diagrammatically in figures 10 and 12.

In observing the flow of blood through these vessels by transillumination of the living animal one is struck by the very rapid flow in the arteries and systemic capillaries and the abrupt slowing of the flow in the larger veins and sinusoids. This is evidently correlated with a change in the blood pressure within these vessels, a change which in turn is correlated

with the fact that all arteries have relatively thick and firm walls, while the capillaries, smaller veins and all sinusoids have extremely thin walls consisting of little tissue other than the intima of the vessels.

This remarkable arrangement of networks of endocranial sinusoids which envelop the brain stem and penetrate its cavities accompanying the greatly enlarged chorioid plexuses presents unique opportunities for the investigation of some fundamental physiological problems. The relations of the blood and the rate of its flow to the composition and movements of cerebrospinal fluid can be studied by direct observation under a wide variety of experimental conditions which give promise of fruitful results.

LITERATURE CITED

- BEDDARD, FRANK E. 1905 A contribution to the knowledge of the encephalic arterial system in Sauropsida. *Proc. Zool. Soc., London*, vol. 2, pp. 59-70.
- BETHGE, E. 1898 Das Blutgefäßsystem von *Salamandra maculata*, *Triton taeniatus* und *Spelerpes fuscus*. *Zeit. f. wiss. Zool.*, Bd. 63, S. 680-707.
- BOAS, J. E. V. 1882 Über den *Conus arteriosus* und die Arterienbogen der Amphibien. *Morph. Jahrb.*, Bd. 7, S. 488-572.
- BURCKHARDT, R. 1891 Untersuchungen am Hirn und Geruchsorgan von *Triton* und *Ichthyophis*. *Zeit. f. wiss. Zool.*, Bd. 52, H. 3, S. 369-403.
- DEMPSTER, W. T. 1930 The morphology of the amphibian endolymphatic organ. *J. Morph.*, vol. 50, pp. 71-126.
- DENDY, ARTHUR 1909 Intracranial vascular system of *Sphenodon*. *Phil. Trans. Roy. Soc. London*, series B, vol. 200, pp. 403-426.
- ECKER, A., R. WIEDERSHEIM AND E. GAUPP 1899 *Anatomie des Frosches*. 2 Auf., 2 Abt., Braunschweig.
- GILMORE, R. J., AND F. J. FIGGE 1929 Morphology of the blood vascular system of the tiger salamander (*Amblystoma tigrinum*). Heart and aortic arches. Colorado College Publication, Genl. Series, no. 161, pp. 1-14.
- HERRICK, C. JUDSON 1924 The amphibian forebrain. I. *Amblystoma*, external form. *J. Comp. Neur.*, vol. 37, pp. 361-372.
- 1927 The amphibian forebrain. IV. The cerebral hemispheres of *Amblystoma*. *J. Comp. Neur.*, vol. 43, pp. 231-325.
- 1933 Morphogenesis of the brain. *J. Morph.*, vol. 54, pp. 233-258.
- 1934 The endocranial blood vascular system of *Amblystoma*. *Zeits. f. mikr.-anat. Forsch.*, Bd. 36, S. 540-544.
- HOCHSTETTER, FERDINAND 1888 Beiträge zur vergleichenden Anatomie und Entwicklungsgeschichte des Venensystems der Amphibien und Fische. *Morph. Jahrb.*, Bd. 13, S. 119-172.

- HOFMANN, MAX 1900 Zur vergleichenden Anatomie der Gehirn- und Rückenmarkarterien der Vertebraten. Zeit. f. Morph. und Anthroph., Bd. 2, S. 247-322.
- KAPPERS, C. U. ARIËNS 1933 The forebrain arteries in plagiostomes, reptiles, birds, and monotremes. Proc. Roy. Acad., Amsterdam, vol. 36, pp. 52-62.
- KNISELY, MELVIN H. 1934 Apparatus for illuminating living tissue and measuring rate and volume of blood flow (abstract). Anat. Rec., vol. 58, Suppl., p. 73.
- MAURER, FRIEDRICH 1888 Die Kiemen und ihre Gefäße bei anuren und urodelen Amphibien und die Umbildungen der beiden ersten Arterienbögen bei Teleostiern. Morph. Jahrb., Bd. 14, S. 175-222.
- MILLER, WILLIAM S. 1900 The vascular system of *Necturus maculatus*. Bull. of the Univ. of Wisconsin, no. 33, pp. 211-226.
- OSAWA, GAKUTARO 1902 Beiträge zur Anatomie des japanischen Riesensalamanders. Mittheilungen a. d. med. Facultät der Kaiserlich-Japanischen Univ., Tokio, Bd. 5, S. 221-427.
- REESE, ALBERT M. 1906 Anatomy of *Cryptobranchus allegheniensis*. Am. Nat., vol. 40, pp. 287-326.
- REX, HUGO 1892 Beiträge zur Morphologie der Hirnvenen der Amphibien. Morph. Jahrb., Bd. 19, S. 295-311.
- SCHÖBL, D. JOS. 1882 Ueber die Blutgefäße des cerebrospinalen Nervensystems der Urodelen. Archiv f. mikr. Anat., Bd. 20, S. 87-92.
- STREETER, GEORGE L. 1916 The vascular drainage of the endolymphatic sac and its topographical relation to the transverse sinus in the human embryo. Am. J. Anat., vol. 19, pp. 67-89.
- WARREN, JOHN 1905 The development of the paraphysis and the pineal region in *Necturus maculatus*. Am. J. Anat., vol. 5, pp. 1-27.

